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THE LATE CRETACEOUS COLEOID CEPHALOPOD
ACTINOSEPIA CANADENSIS WHITEAVES

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ABSTRACT

Eighteen new specimens and seven of eight previously reported specimens of the coleoid fossil *Actinosepia canadensis* Whiteaves provide data for redescription and interpretation. The monotypic genus is known only from Late Campanian and Maastrichtian strata in the northern Great Plains region of the United States and Canada. Its gross morphology and shell structure require its inclusion in the teuthidid family Trachyteuthidae, but also suggest relationship, possibly ancestral, to the sepiids.

INTRODUCTION

Parts of eighteen individuals of the rare coleoid cephalopod *Actinosepia canadensis* Whiteaves, are among a large collection of invertebrate fossils gathered during studies of the Fox Hills Formation (Maastrichtian) in South Dakota and Wyoming. Only 8 specimens of *Actinosepia* have been reported previously, all of these are also from the Late Cretaceous of the western interior of North America. The specimens are in various stages of preservation and none are perfect. Collectively they permit a more detailed

morphologic description than now exists for *Actinosepia*. Certain aspects of the shell and its structure raise questions concerning the systematic position of this monotypic genus, and features of its distribution in the Fox Hills Formation suggest habits differing from those of its cephalopod contemporaries.

The dominantly corneous shell of *Actinosepia* is broad, transversely arched, and concave ventrally in its posterior part, the whole resembling the inverted bowl of a spoon (fig. 1). In this respect and in certain details of its structure it is similar to the dorsal layers of the shell of *Sepia*, but it differs markedly from the sepioid shell as a whole in lacking the characteristic spongy, ventral pad of chalky lamellae. Naef (1922, p. 135) interpreted similar sepia-like coleoid shells that lack a ventral pad as teuthidids (Mesoteuthoidea) and extended the term gladius to apply to them as well as to the more familiar, slender teuthoid "pens" to which the term was originally applied. Gladius, as used here in reference to the shell of *Actinosepia*, is a general term applicable to any dominantly corneous, internal coleoid shell that lacks either a calcareous pad or a true phragmocone. The term pad, a direct translation of the German term *Wulst*, employed by Appellöf (1893) in his classic work on the shell of *Sepia*, is used in preference to the more common "phragmocone" because the latter is an incorrect and subjective extension of a useful term in cephalopod morphology. The sepioid pad perhaps may be homologous with part of the cephalopod phragmocone but it is not in itself a chambered cone.

For encouraging this redescription of *Actinosepia*, I am indebted to Dr. J. A. Jeletzky who made possible the loan of the holotype and other specimens from the Geological Survey of Canada. Dr. Jeletzky kindly read the manuscript, although his views on coleoid phylogeny do not agree with the origin of sepiids suggested as a possibility herein. I have profited from discussions of shell structure with Dr. Copeland MacClintock and from his critical reading of the manuscript. I also wish to thank Drs. W. G. E. Caldwell, W. A. Cobban, A. W. Fischer, R. W. Landes, L. S. Russell and N. F. Sohl for their efforts in helping me locate

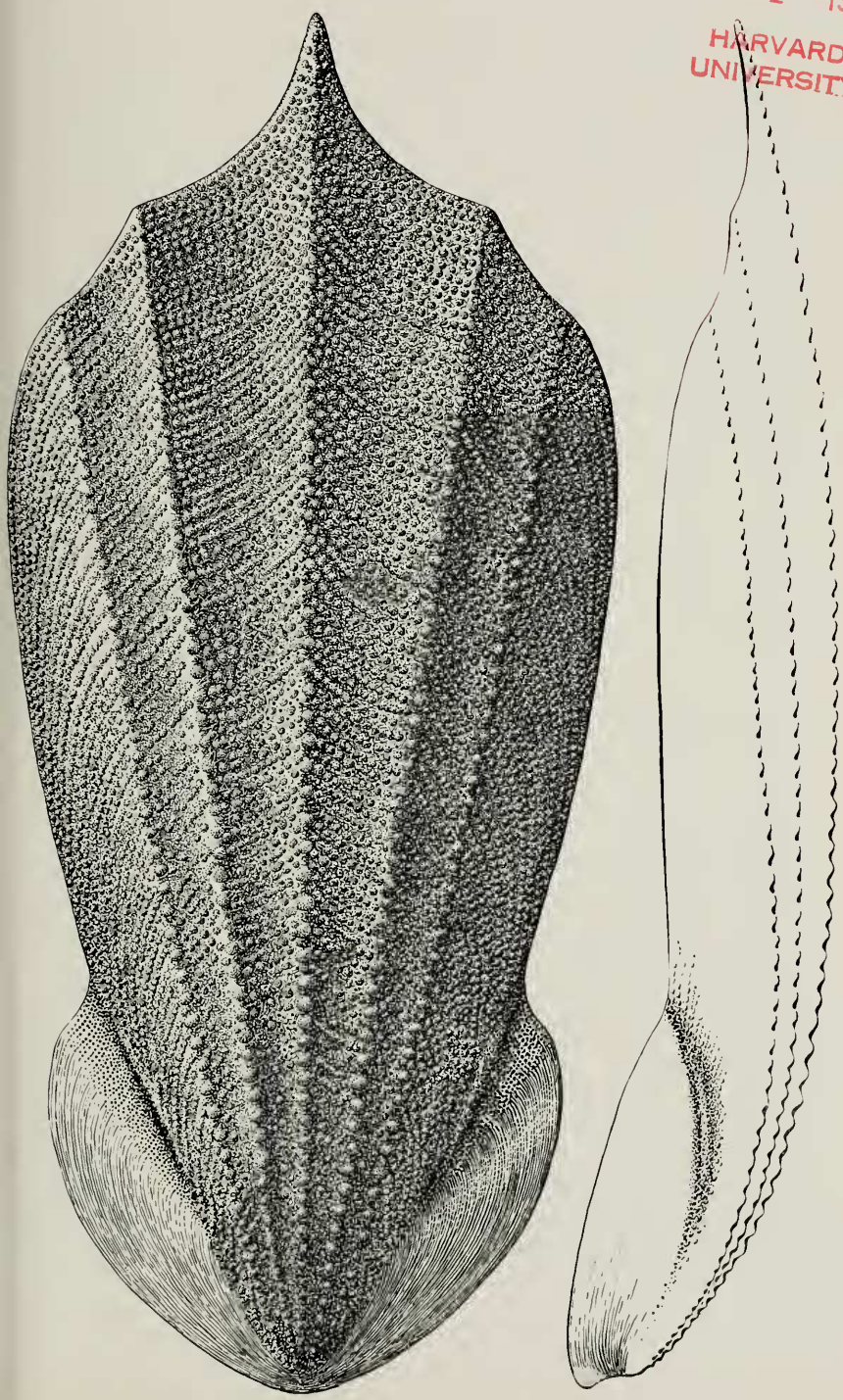
Figure 1. Reconstruction of *Actinosepia canadensis* Whiteaves: dorsal aspect and longitudinal profile. Approximately $\times \frac{3}{8}$. Based largely on GSC 19888 (Pl. 2). Drawn by Carl Wester.

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all but one of the known specimens for this study. Martha Dimock, David Keith and Michael Waldman assisted with preparation of specimens and illustrations; the reconstruction of *Actinosepia* was drawn by Carl Wester. Grants from the National Science Foundation (G-5657, G-18674) that made possible the study of the Fox Hills Formation and its faunas are gratefully acknowledged.

OCCURRENCE

Specimens of *Actinosepia canadensis* have been reported previously from three localities; this paper records their occurrence at three additional localities, one of which is a fairly large area that includes a number of individual sites. The distribution and stratigraphic position of these localities is shown in fig. 2. The initial report on *Actinosepia* is based on four specimens collected

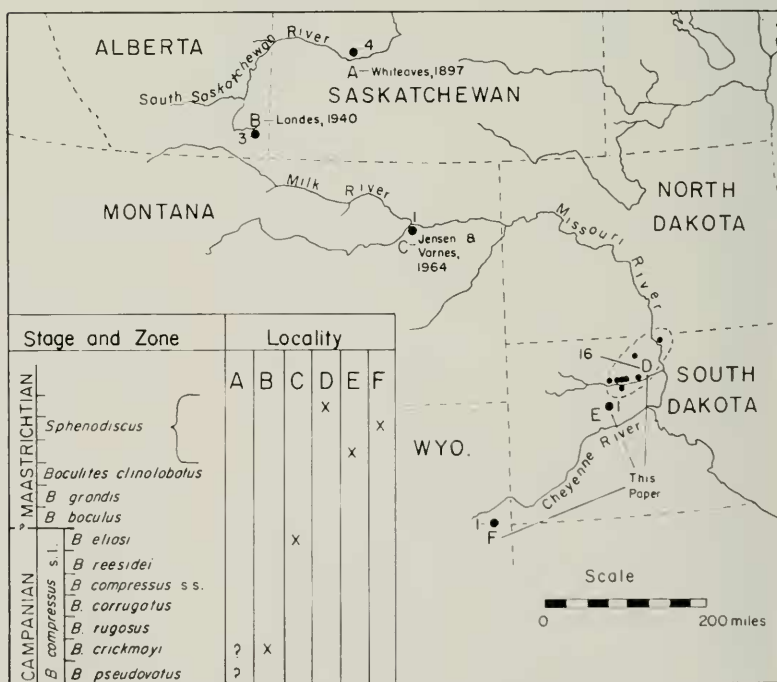


Figure 2. Geographic and stratigraphic distribution of the recorded occurrences of *Actinosepia canadensis*. The baculite zonation is from Cobban (1958b; 1962). Numbers=number of specimens.

“. . . from the Montana or Pierre-Fox Hills formation of the Later North American Cretaceous, at the South Saskatchewan, opposite the mouth of Swift Current Creek.” (Whiteaves, 1897, p. 459). These specimens are undoubtedly from the Bearpaw Shale but the exact horizon within the formation is not known, though it is most likely within the Campanian.

The second occurrence was reported by Landes (1940, p. 180) from the Bearpaw Shale of the Manyberries section in southeastern Alberta (Russell, 1940, p. 76). Here, two partial gladii (one of which was not found in the search for specimens) and a spectacular external mold of a third were found in silty limestone concretions about 290 feet above the base of the formation. From that part of the Manyberries section in which *Actinosepia* was found Russell (1940, p. 81) lists a fauna that includes *Placenticerias meeki*, *P. intercalare*, and *Baculites compressus*. In the paleontologic portion of the same report Landes (1940, p. 173) lists *Baculites crickmayi* from the same locality and same stratigraphic level as the specimens of *Actinosepia*. According to the current classification of the Interior Cretaceous (Cobban and Reeside, 1952) these associations indicate a Late Campanian age for the Alberta specimens.

More recently, Jensen and Varnes (1964, p. F9) found a specimen of *Actinosepia* in the upper Bearpaw Shale near the Fort Peck reservoir in Valley County, Montana. This specimen is from the middle part of what Jensen and Varnes call their upper unit of the Bearpaw, about 100 feet below the top of the formation according to the specimen label. From at or near the same locality that yielded *Actinosepia*, Cobban (1958a, p. 663-664; 1962, p. 126) identified *Baculites eliasi* Cobban in collections made by Jensen from 109 to 174 feet below the top of the formation. Consequently the Montana specimen of *Actinosepia* is either in or just above the *B. eliasi* zone and is either latest Campanian or earliest Maastrichtian in age (fig. 2).

During the current study of the Fox Hills Formation, 16 specimens of *Actinosepia* were found in and adjacent to its type area in north central South Dakota. In addition one specimen was found on an outcrop of the upper part of the Mobridge Member of the Pierre Shale. All of these specimens occur in the range of *Sphenodiscus*, above the zone of *Baculites clinolobatus*, and are

Maastrichtian in age. In the Fox Hills Formation northeast of Lance Creek, Wyoming, a single small fragment, identifiable as *Actinosepia* only because of its unique shell structure, was found in a phosphatic nodule layer associated with fragmental sphenodiscids. The formation is of Maastrichtian age at this locality.

The combined range in age for all the known specimens of *Actinosepia* is Late Campanian and Maastrichtian. The zonation of the Cretaceous based on species of *Baculites* is particularly useful in establishing the relative ages of *Actinosepia* specimens from different localities. Cobban (1962, p. 127) uses collections from the north flank of the Black Hills uplift in Carter County, Montana, to illustrate the “. . . zonation of the older forms of *compressus*-like baculites . . .” in Montana. Here *B. crickmayi* occurs in beds above the *B. pseudovatus* zone and well below the horizon of *B. eliasi*. *B. pseudovatus* marks the base and *B. eliasi* the top of what was originally called the *B. compressus* zone (Cobban and Reeside, 1952, p. 1020-1022). Omitting the Whiteaves material, for which there are no data on either stratigraphic position or associated fossils, the Alberta specimens of *Actinosepia*, reportedly associated with *B. crickmayi*, are the oldest. The Montana specimen from in, or just above, the *B. eliasi* zone is younger than the Alberta specimens but is the oldest specimen known from south of the Canadian border. Two zones separate the *B. eliasi* zone and the *B. clinolobatus* zone; the latter is the highest baculitid zone yet recognized in the Interior (Cobban, 1958b, p. 114), and all the other known specimens of *Actinosepia* occur above it.

With so few occurrences of *Actinosepia* known not very much significance can be attached to the fact that it is found in progressively younger rocks southward. Within their restricted area of distribution the pattern suggests that they migrated slowly southward with the withdrawal of the Cretaceous sea. Geographically the specimens are fairly well distributed throughout the eastern part of that area where the Upper Cretaceous terrain reaches its maximum width astride the international boundary. All of the known occurrences are from highly silty or sandy beds and in view of this, it is strange that none have been found in the sandier western part of the Upper Cretaceous outcrop belt. Again the sample is too small to indicate whether this was environmental preference on the part of the animal, whether conditions for pres-

ervation were optimum in the east, or whether the distribution is merely fortuitous. The outstanding feature of the distribution of *Actinosepia* is the apparent restriction of this predatory cephalopod to so limited an area for so long a time.

PRESERVATION

The specimens of *Actinosepia* are poorly preserved and it is only by comparison of all of them that the nature of the gladius as a whole can be reconstructed (fig. 1). The very slightly calcareous, corneous shell material is thinly laminated and shows two structurally distinct layers. In the inner (ventral) layer the shell laminae are essentially flat; in the outer shell layer the laminae begin flat but develop a characteristic dorsal tubercular structure which stands out as ornamentation on the surface. Fine parallel grooves and ridges that apparently mark increments of growth occur internally where the layers meet. In none of the specimens is there evidence of a ventral pad such as that in living cuttlefish and it can only be assumed that no such structure was present. In fresh specimens the material of the gladius is translucent, conchoidally fracturing and amber to dark brown in color with a resinous lustre. Weathered specimens are commonly mottled white and bluish-gray and are porcelaneous in appearance.

Other than the four specimens collected by Whiteaves from the South Saskatchewan River and two fragments, including that from Lance Creek, Wyoming, each fossil gladius of *Actinosepia* occurs singly in somewhat flattened, ovoid, calcareous concretions that are most commonly barren of other fossils (Pl. 1, fig. 4). Most of the concretions are slightly to significantly smaller than the enclosed gladius, the posterior end and front edge of which are usually missing. All of the gladii show some signs of decomposition and many are riddled with holes and frayed about the edges. Flakes of the corneous material are common in the matrix surrounding many of the specimens in which decomposition is marked. Disintegration of the shells appears to have occurred by the progressive separation of shell laminae, in a manner similar to the exfoliation of the horns of cattle on dessication. Thin sections of many *Actinosepia* gladii show matrix or secondary mineral matter between exfoliating outer layers and the body of the gladius.

Although individual specimens are commonly fragmental within their concretions, relatively few show separation or rotation of the parts. Five specimens from the Fox Hills Formation were collected in place from a single locality; in all of these the plane of the gladius was parallel to the bedding and the convex side was up. Even where some pieces of *Actinosepia* have been rotated the general orientation of the whole gladius parallel to the bedding is evident. Associated sedimentary structures indicate that stirring of sediment by burrowing organisms most likely accounts for the rotation of pieces. Only the isolated, worn fragment from the phosphatic nodule bed of the Fox Hills Formation at Lance Creek, Wyoming, is obviously transported. The more complete specimens of *Actinosepia* show no evidence of having been transported. What appears to have been the natural concavity of the spoon-shaped gladius is preserved in most of the specimens found in concretions. Apparently calcification of the matrix around the specimen to form the enclosing concretion occurred before there was sufficient sediment load to compress the gladius.

Whiteaves' specimens from the South Saskatchewan occur in a fine-grained, glauconitic sandstone firmly held together on the underside of the specimens by ferruginous cement. Whether they occurred in ferruginous concretions or were individually carved out of an indurated bed of sand is not known. On all of these specimens, including the holotype, the dorsal tuberculate shell layer is missing except for a few very small scraps but it is not possible to tell whether this is the result of decomposition prior to preservation or an artifact of collection.

Poor as most of them are, the specimens of *Actinosepia* must be considered as examples of rather unusual conditions of preservation in view of the rarity of preservation of the organic inner shells of coleoid cephalopods in general. The material of the gladius is much more decomposed than the shells of associated molluscs and crustaceans. One concretion from the Fox Hills Formation in the type area has a single protobranch bivalve in addition to the coleoid gladius. The gladius, though preserving its original convexity, is considerably disintegrated and only patches of the inner layers of the shell remain. The pelecypod shell, on the other hand, is excellently preserved. Numerous small concretions from the same beds as the coleoid concretions in the type area of

the Fox Hills contain ammonites, pelecypods and crab claws with their respective shells in good to excellent states of preservation, the ammonites even showing the iridescent inner layers of nacre.

Schaffer (1958, p. 146-147) stressed the importance of recognizing different states of preservation for correct systematic evaluation of Tertiary sepiid remains and in some measure this warning can be applied to specimens of *Actinosepia*. Although strong ribs radiating from the posterior end of the elongate-ovoid gladius are diagnostic for the genus, appreciable variation in the appearance of two specimens can result if mostly outer laminae of the shell are preserved in one and mostly inner laminae in the other. Three *Actinosepia* specimens from the South Dakota collections show no trace of the outer tubercular shell layer. All of these are from the same locality and horizon as specimens preserving some of the tubercular layer. A number of other *Actinosepia* specimens, among them Whiteaves' holotype, have only small patches of this layer remaining. The majority of specimens, including both the oldest and youngest known, have parts of both layers preserved. Accident of preservation, rather than taxonomic or dimorphic difference, is indicated for those specimens of *Actinosepia* that lack shell laminae with tubercular structure.

LOCAL PATTERN OF DISTRIBUTION

Detailed studies of fossil distribution are available for the Fox Hills Formation in its type area where 16 of the 26 specimens of *Actinosepia* have been found. Even in this area of relative abundance it is an uncommon and numerically unimportant element in the Fox Hills fauna, but the peculiarity of its local distribution relative to other invertebrate contemporaries is of interest for what it may eventually reveal of the habits and habitat of the animal.

Of the 16 specimens from the Fox Hills 12 were collected in place, the remainder from float. Nine of the specimens in place were found at the same stratigraphic level within a limited area of outcrop and three of the float specimens are also from this area and presumably from the same horizon, so nearly half of all the known specimens of *Actinosepia* apparently were part of a single community.

The rather complex nature of fossil distribution in the Fox Hills Formation in its type area is described elsewhere (Waage, 1961; 1966). Briefly, the lower part of the formation, which is a clayey silt, locally contains successive layers of calcareous concretions, many of them rich in excellently preserved fossils. The fossil assemblages of the individual layers, or groups of layers, are characteristically dominated by great numbers of one or two molluscan species. Because the dominant species differ from layer to layer the successive assemblages are individually distinctive; they maintain their stratigraphic position relative to one another throughout their area of occurrence. We are concerned here only with the four assemblages in the lower 50 feet of the Fox Hills Formation, in the lower part of the Trail City Member. The succession is shown diagrammatically in fig. 3 along with a map showing the distribution of fossils at the horizon of the *Actinosepia* concentration.

One of the outstanding features of the four fossil assemblages is their geographic restriction to an elongate northeast-trending area that occupies only a part of the exposures in the type area of the Fox Hills Formation. These four successive assemblage zones have slightly different limits, but all fall within the same general area. The assemblages in the different layers bear a marked resemblance to natural bottom communities and they have been interpreted as resulting from recurrent mass mortalities of successive communities with little subsequent reworking (Waage, 1966).

The relation of the lobate area of fossil accumulation to local oceanographic conditions is revealed upward in the Fox Hills sequence. Starting in the northern part of the lobate area during the accumulation of the *Protocardia-Oxytoma* Assemblage Zone a sand facies encroaches from the north and northeast, its early stages lying within the lobate area and later stages overspreading it but retaining the approximate NNE trend in both its axis of greatest thickness and the lineation of its abruptly terminated western edge. Within this sand body, the Timber Lake Member, varying marine biofacies show progressive change to more restricted faunas both upward and northward. To the west it grades into lagoonal deposits, on the east its outcrop is truncated by recent erosion. The encroachment of this sand barrier from the NNE over the site of the lobate area of successive fossil accumulations suggests that a

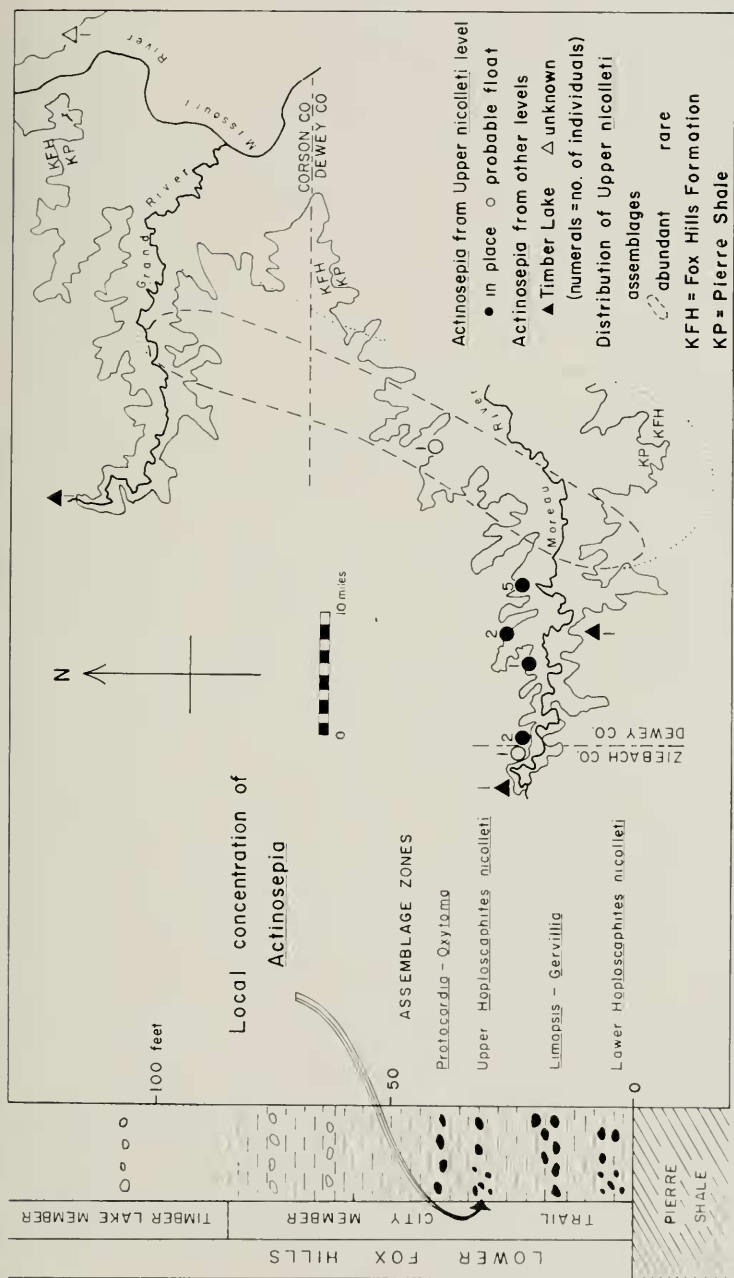


Figure 3. Stratigraphic and geographic distribution of *Actinosepia canadensis* in the Fox Hills Formation, type area, northwest-central South Dakota.

current flowing southwestward through the area was a critical factor in the periodic local presence of a rich bottom fauna. Other paleogeographic features indicate that open sea lay to the south and ESE of the lobate area.

The majority of *Actinosepia* specimens come from the horizon of the Upper *nicolleti* Assemblage Zone and their geographic concentration (see fig. 3) is west of the southwestern end of the area occupied by the Upper *nicolleti* accumulations. The Upper *nicolleti* Assemblage Zone is the second of two levels of rich fossil assemblages characterized by an abundance of the scaphitid ammonoid *Hoploscaphites nicolleti*; it is restricted to a smaller area of distribution than the other assemblages in the lower 50 feet of the Fox Hills Formation. The more common associates of *H. nicolleti* in the upper assemblage are two or three other scaphitids of the genus *Discoscaphites*, and the pelecypods *Oxytoma nebrascana*, *Protocardia subquadrata* and *Inoceramus fibrosus*. Within the Upper *nicolleti* Assemblage Zone the fossils occur in scattered large calcareous concretions up to as much as 20 inches in diameter. The zone also includes some small ovoid concretions, generally barren of fossils. At the abrupt western edge of the Upper *nicolleti* assemblages in the Moreau River valley the zone changes to an interval from four to eight feet thick, containing numerous small, round to ovoid concretions most of which are unfossiliferous; the *Actinosepia* specimens are from concretions in this interval. In the Grand River valley to the north the situation is not parallel, inasmuch as the Upper *nicolleti* zone pinches out westward and its laterally equivalent interval of small concretions is missing from the section, presumably because of nondeposition.

Species associated with *Actinosepia* in the interval of small concretions are mostly the ammonoids *Hoploscaphites nicolleti*, *Discoscaphites cheyennensis*, and a large *Discoscaphites* related to *D. nebrascensis*. A few clusters of *Oxytoma nebrascana* occur in the small concretions near the west edge of the Upper *nicolleti* assemblages but pelecypods, other than a few scattered proto-branches, are exceedingly rare. A few of the concretions contain claws and carapaces of crustaceans. Fragments of fossil wood also were found, including a ten-foot section of the slender trunk of what is possibly a sabaloid palm (Delevoryas, 1964, p. 585). As the interval of small concretions was not collected systematically

throughout its area of outcrop but only sampled at a few localities the frequency of occurrence of *Actinosepia* is not known. At the locality where five specimens were found (see fig. 3) the outcrop of the interval was searched more thoroughly and over a greater area, approximately half a square mile of intricately dissected river bluffs. The density of *Actinosepia* specimens is thus not great and there is no indication from the fossil distribution that they were gregarious; in this respect they contrast markedly with their ammonoid neighbors to the east, *Hoploscaphites nicolleti*, whose fossil masses at the same horizon indicate that they were swarming at the time of their death.

Although specimens of *Actinosepia* are few, their geographic grouping at a particular stratigraphic level takes on significance in the context of the strongly patterned distribution of fossils demonstrated for the type Fox Hills. The obvious feature in their distribution at the Upper *nicolleti* level is the location of all but one of the 12 specimens in an area peripheral to rather than within the lobate area of abundant fossil accumulation (fig. 3). The almost complete lack of a molluscan bottom fauna in the peripheral area suggests that bottom conditions were relatively inhospitable and raises the possibility that *Actinosepia gladii* were preserved here but destroyed by organic activity in the adjacent area with abundant benthic molluscs. The facts do not support this possibility. The conspicuous break in mollusc distribution is misleading, as the beds in the peripheral area show the same degree of reworking of sediment by organisms as do those in the highly fossiliferous area. Irregular grade-size mixing, contorted laminae and burrows are common features of the matrix of *Actinosepia* concretions as well as of the surrounding sediment, and in thin section organic sediment sorting and fecal pellets are abundantly visible.

If the fossil accumulations in the Fox Hills Formation reflect the original distribution of living organisms, as is believed (Waage, 1966), and the distribution of *Actinosepia* is not the result of selective preservation, it is reasonable to suspect that *Actinosepia* preferred areas peripheral to those with populous molluscan communities. Possible reasons for such a preference are numerous but owing to the general lack of even suggestive evidence their recitation would be unrewarding. The only empirical data that may bear on the problem are distributional and concern cephalopod

contemporaries of *Actinosepia*. These are present in abundance and variety enough to direct attention to competition as a possible factor in the local distribution of *Actinosepia*.

Ammonoids of two kinds, scaphitids and sphenodiscids, make up from 95 to over 99 per cent of the cephalopod fauna in the fossil assemblages of the Fox Hills Formation; scaphitids alone constitute 67 to 99 per cent of the cephalopod fauna in the four lower assemblage zones of the formation (fig. 3). The non-ammonoids that make up the remaining five per cent or less of the cephalopod fauna are *Belemitella bulbosa*, *Nautilus dekayi*, and *Actinosepia*. Unlike *Actinosepia*, which in the lower Fox Hills is found only at the Upper *nicolleti* level, the other non-ammonoid cephalopods are a consistent though minor element in all assemblage zones. For the four assemblage zones in question, the percentage of non-ammonoids in the cephalopod faunas from the area of abundant fossils is as follows: Lower *nicolleti*—0.8 per cent; *Limopsis-Gervillia*—5.1 per cent; Upper *nicolleti*—1.5 per cent; *Protocardia-Oxytoma*—2.2 per cent. If its peripheral area were included the non-ammonoid percentage for the Upper *nicolleti* Assemblage Zone would be raised to nearly five per cent by the concentration of *Actinosepia*.

Counts of the cephalopod elements at the Upper *nicolleti* level are given in Table 1, the localities represented include all the non-ammonoid cephalopods found at that horizon. If the distribution of *Actinosepia* was influenced by a contemporary cephalopod the numerically dominant scaphitids, particularly *H.*

TABLE 1. Count of cephalopod specimens from collections in and peripheral to the area of abundant fossils at the horizon of the Upper *nicolleti* Assemblage Zone.

CEPHALOPODS	NUMBER OF SPECIMENS	
	From 12 localities in the area of <i>nicolleti</i> assemblages	From 12 localities in the area peripheral to <i>nicolleti</i> assemblages
<i>Hoploscaphites nicolleti</i>	202	7
Other scaphitids	56	12
<i>Sphenodiscus</i>	3	0
Nautiloids	2	0
Belemnoids	1	0
<i>Actinosepia</i>	1	11

nicolleti, are the obvious candidates. The relative rarity of the other non-ammonoid cephalopods make them unlikely candidates. The percentage of non-ammonoids in the cephalopod fauna is lowest in the two assemblage zones that feature an unusual abundance of *H. nicolleti* and this together with the fact that these same two zones have the highest percentage of cephalopod specimens in the total fauna (8.8 and 15.1 for the Lower and Upper *nicolleti* zones respectively) suggests that the apparent local swarming of *H. nicolleti* may have had a significant effect on all other cephalopods.

The close parallel in molluscan associations, both ammonoid and pelecypod, between the Upper and Lower *nicolleti* assemblages leads one to expect to find *Actinosepia* in the areas peripheral to the Lower *nicolleti* zone, which like the Upper also changes laterally to an interval with small, generally barren, concretions. But *Actinosepia* has not been found at this horizon although its presence in the underlying Pierre Shale within 30 miles of the area of Fox Hills fossil assemblages indicates that it had previously appeared as a member of the regional fauna.

In summary, *Actinosepia* appears to have been only an occasional inhabitant of the shallow coastal waters in which the type Fox Hills Formation was deposited. Its relatively abundant remains at one horizon are concentrated in otherwise nearly barren beds peripheral to, and on the shoreward side of, a rich molluscan biofacies. The coincidence of this locally restricted occurrence with unusually high productivity of the scaphitid *H. nicolleti* in the adjacent molluscan biofacies may be significant. However, except for one obviously transported specimen, none of the gladii of *Actinosepia* known have been found directly associated with an abundance of other fossils.

SYSTEMATIC DESCRIPTION

CLASS CEPHALOPODA

SUBCLASS COLEOIDEA Bather 1888

ORDER TEUTHIDIDA Naef 1916

FAMILY TRACHYTEUTHIDAE Naef 1921

Diagnosis: Broad teuthidid gladii with tubercular structure in outer shell laminae over median or greater part of dorsal area;

Late Jurassic (*Trachyteuthis*, *Voltzia*) and Cretaceous (*Glyphiteuthis*, *Libanoteuthis*, *Actinosepia*).

Discussion: According to Naef's diagnosis trachyteuthids are "bulky mesoteuthoids whose more or less *Sepia*-like shells are strongly calcified and show knobby roughness on the dorsal mid-region." (1922, p. 136-137; translation.) In effect, Naef includes in the Trachyteuthidae all teuthidids whose dorsal shell layer shows tubercular structure in any part. All such species appear to have had relatively broad, sturdy gladii, but the degree of calcification varies considerably even within a single gladius and contrary to Naef's implication it is not a diagnostic feature of trachyteuthid gladii. In addition to the type genus, *Trachyteuthis* von Meyer, Naef (1922, p. 136-141) included *Glyphiteuthis* Reuss in the family. Subsequently Kretzoi (1942, p. 134) erected the genus *Libanoteuthis* to include the Lebanese Late Cretaceous species *Trachyteuthis libanotica* (Fraas)¹, a device that leaves only European Late Jurassic species in *Trachyteuthis*. *Glyphiteuthis* is known only from the Late Cretaceous of Czechoslovakia.

With the inclusion of *Actinosepia* the family Trachyteuthidae becomes a receptacle for Mesozoic coleoid gladii that have tubercular shell structure but lack a ventral pad or other kind of phragmoconal part. Whether the family so defined has any validity as a natural group is questionable. The genera noted have characteristics other than tuberculation in common; chief among these are 1) the lack of separation of the gladius into middle and side plates by asymptotes and 2) the restriction of broadly rounded conus vanes to half or less of the gladius length. These features are no more indicative of genetic relationship than is the tuberculation. Trachyteuthid genera may be related or they may represent variants of more than one teuthidid stock that took to shallow coastal waters and a *Sepia*-like mode of life. If one accepts the independent development of tuberculation in sepiids and in teuthidids one must also admit the possibility of its independent development in different teuthidid stocks.

¹ Bülow-Trummer (1920, p. 255) refers *Geoteuthis libanotica* Fraas, the original designation of the type species of *Libanoteuthis*, to the "Lias," but Roger (1946, p. 6, 17) notes that Fraas' specimen from Hakel and specimens found subsequently at Sahel-Alma are respectively from rocks of Cenomanian and Senonian age.

Voltzia palmeri Schevill from the Late Jurassic of Cuba is added provisionally to the trachyteuthids, bringing within the group all tuberculate gladii described to date from the Mesozoic. The provisional status of the assignment stems from the possibility that *Voltzia* is synonymous with *Trachyteuthis* and not from the fact that it was described as a sepiid. The specimen of *Voltzia palmeri* is not available but neither the text nor the illustrations of Schevill's (1950) description contain evidence that it possessed a pad. What Schevill calls the "phragmocone" is apparently only the filling of a ventral concavity in the central part of the gladius, for in describing the phragmoconal deposit he states (1950, p. 100), "detailed structure not apparent in this material because of bituminous replacement, as is frequent in other fossils from this locality." Similar axial, ventral concavities in the gladius are observable in many specimens of *Trachyteuthis hastiformis* (Rüppell), the common Solenhofen species, and are obviously filled with matrix which may protrude dorsally as an elongate-oval mound where the substance of the gladius has been removed. That this concavity in *Trachyteuthis* was not occupied by a calcified pad at the time of burial is indicated by the presence of small holdfasts attached to the ventral surface, usually near the axis of the concavity.² The specimen of *Voltzia palmeri* needs careful restudy; Schevill himself pointed out its superficial resemblance to *Trachyteuthis*, and one supposes that he would have referred it to this genus had he not believed that the bitumen-filled, raised area in the center of his specimen was a pad.

GENUS *ACTINOSEPIA* Whiteaves 1897

Type species: *Actinosepia canadensis* Whiteaves, 1897, by monotypy.

Emended diagnosis: Gladius broad, ovoid, arched, with ventral concavity deepening posteriorly; consists of large main body undivided by asymptotes with rounded conus vane flanking

² In his original description of *Trachyteuthis*, von Meyer (1846) notes these holdfasts and attributes them to erinoids; whatever their nature they are a common feature of the Solenhofen trachyteuthids; a good specimen showing the holdfasts and the nature of the axial, ventral concavity in *Trachyteuthis* is in the U. S. National Museum (USNM 16622).

rear third along weak lateral asymptote. Main body expands forward fan-like from apex, attains maximum gladius width about one-third length from anterior end; dorsally, five narrow, longitudinal ribs radiate from apex, the stronger median rib protrudes beyond anterior margin in an acuminate tip, weaker laterals impart slight scallop to margin. Gladius substance corneous to corneous-calcareous, in two laminated layers, the ventral smooth, the dorsal with outer laminae tuberculate. Surface of gladius ornamented with fine to coarse tubercles except on conus vanes. Apex poorly known; rostrum, if any, small. *Range*: Late Campanian and Maastrichtian.

Distribution: Great Plains region of southern Canada and northern U.S.A.

Discussion: The ovoid plan of the gladius, its five radiating ribs and its acuminate tip were Whiteaves' basis for suggesting that the coleoid specimens from the South Saskatchewan River "... seem to indicate a new genus and species of Sepiidae, for which the name *Actinosepia Canadensis* may not be inappropriate." (1897, p. 460.) The principal addition to this definition is the presence of an outer layer of tuberculate shell laminae and the resultant nodular ornamentation of most of the dorsal surface of the gladius; a feature noted by Landes (1940, p. 180) on the Alberta specimens but not evident on the four exfoliated specimens available to Whiteaves. *Actinosepia* cannot be classed as a sepiid, as Whiteaves did, for in spite of its many *Sepia*-like characters it lacks the ventral pad definitive of that group. As a teuthidid, the tubercular structure justifies its inclusion in the family Trachyteuthidae

ACTINOSEPIA CANADENSIS Whiteaves

Fig. 1; Pl. 1, 2, 3, and 4a, b, c.

Actinosepia canadensis Whiteaves, 1897, p. 459-460, pl. 2; Landes, 1940, p. 180-181.

Material and Measurements: Table 2 lists dimensions and rib angles for the ten more complete specimens of *A. canadensis*. The dimensions are at best approximations and not direct measure-

ments. The external mold, GSC 19888 (see Pl. 2), collected by Landes and used by him (1940, p. 180) in his description, retains more of the form and external ornamentation of the gladius than any other specimen and is the only one preserving the posterior end with the vanes. The length of other specimens was estimated by matching their greatest measurable rib spacing with the corresponding spacing on GSC 19888 and measuring the distance along the median rib of the latter from the match point to the posterior end. To this was added the length of gladius preserved (or recon-

TABLE 2. Measurements of the ten most nearly complete specimens of *Actinosepia canadensis*. The estimated measurements are considered minimal. For method of estimation see p. 19.

SPECIMEN	Estimated length (cm)	Estimated width at anterior maximum (cm)	Median-inner rib angle	Median-outer rib angle
Bearpaw Shale Saskatchewan Whiteaves (1897)				
GSC 5379 (holotype)	21	8.5	7°	10°
GSC 5379a	22+	11.0	6° to 6.5°	—
GSC 5379b	22.0	11.0	6°	—
GSC 5379c	21+	—	6.5°	—
Bearpaw Shale Alberta Landes (1940)				
GSC 19888	30	12.5	8° to 8.5°	12°
GSC 16395	21	10.0	7.5°	—
Bearpaw Shale Montana Jensen and Varnes (1964)				
USNM 147231	18.2	8.0	6° to 7°	—
Fox Hills Fm. South Dakota (This paper)				
YPM 24809	23.0	9.4	8°	12.5° to 13°
YPM 24808	20.0	8.6	8°	12.5° to 13°
YPM 24811	—	—	8.5°	15°

structed by extension of growth lines across the median rib) anterior to the match point on the specimen being compared. The sum of these two measurements provides an approximate minimum length. Measurement of maximum width is even less accurate as the lateral edges of the gladius are commonly frayed, curled or flattened. The four specimens whose dimensions are judged to be more reliable are GSC 19888, GSC 5379, YPM 24809 and YPM 24808; height-width ratio of these specimens is from 2.3 to 2.5. Features of the anterior half of the gladius are based chiefly on GSC 5379, GSC 5379b, GSC 16395, YPM 24808 and YPM 24809. Data on shell structure and ornamentation came mostly from GSC 19888, USNM 147231, YPM 24811, YPM 24812, and YPM 24810. (YPM = Yale Peabody Museum; GSC = Geological Survey of Canada; USNM = United States National Museum.)

Description: Gladius approximately 2.5 times as long as its maximum width. Range of estimated minimum length of ten best-preserved specimens is 18 to 30 cm. Main body of gladius gently arched transversely; the amount of convexity varies and probably is affected by mode of preservation; in GSC 19888 height/width = 0.20, in YPM 24809 $h/w = 0.22$, both these specimens are preserved in calcareous concretions and appear to retain their original form. The gladius also has a broad asymmetrical arch longitudinally, the apex being approximately one third length from posterior end so that curvature is markedly greater on posterior third. (see profile, fig. 1). Five dorsal ribs on the the main body are folds in the gladius that appear as shallow grooves on ventral surface; median rib and adjacent ribs on either side, the inner rib pair, are sharp flexures that stand out prominently from apex to anterior margin, median generally higher and broader than the inner ribs; the outer rib pair are slight flexures that commonly become faint toward anterior margin, particularly on inner shell layers. Inner ribs diverge forward from median rib at angles varying from 6 to 8.5 degrees, outer ribs at angles varying from 10 to 15 degrees. Inner ribs lie nearer outer ribs at approximately two thirds the distance from the median rib to the outer ribs.

Ornamentation consisting of tubercles of various size and irregular ridges of coalesced tubercles covers the dorsal surface of the

main body of the gladius. Ribs bear large, closely-spaced tubercles, asymmetrically inclined forward and rounded on top; on the bigger *A. canadensis* specimens these are as much as 3 mm in diameter at the base; some show annular pattern of growth laminae on blunt tops (Pl. 3, fig. 3) indicating either wear or resorption—but most likely the latter, as can be demonstrated for the dorsal tuberculate shell layer in *Sepia* cuttlebones. Ornament on intercostal areas begins as crowded rows of small tubercles, usually 1 mm or less in size, that closely parallel growth lines; as these grow with the addition of new shell laminae they impinge on one another, the ornament pattern becoming increasingly irregular as tubercles grow differentially and/or fuse to form anastomosing nodular ridges (Pl. 3, fig. 2). Ornament between inner and outer ribs becomes finer and arrangement of tubercles along growth-lines is obvious even on large gladii; tubercles decrease gradually in size as their rows swing backward with growth lines along lateral edge of main body of gladius. Ornament arises from tubercular structure of outer shell laminae. Where inner laminae are exposed they are smooth or show fine, closely-spaced growth ridges or "lines" which are bent sharply forward along median rib, indicating an acuminate tip. From median rib growth lines curve gently backward and outward to inner rib where they are flexed abruptly backward at an angle of about 40 degrees to longitudinal axis of gladius; at outer rib they flex slightly laterally then curve steeply into the lateral margin of gladius.

Lateral vanes border posterior third of gladius, curve downward and outward connecting under apex of main body; their combined outline viewed dorsally is nearly semicircular. Along anterior third of juncture of vanes and main body vanes are downwarped to form broad groove that tapers out backward; groove is flanked by narrow tapering ridge along main body (Pl. 3, fig. 1). Lateral asymptotes follow inner side of groove and continue backward along juncture of vanes and main body; these are the only pair of asymptotes on gladius. Ornament of very fine tubercles spreads into groove from main body, following pattern of growth lines, but does not extend beyond, where vanes are smooth except for fine growth lines that parallel their periphery. In the one specimen preserving vanes (GSC 19888) they appear thinner than shell of main body.

The matrix bearing the posterior end of the gladius in GSC 19888 was X-rayed and excavated as far as possible without destroying it, but no rostrum was found. Some thickening of shell at apex is apparent and the area has been worn or exfoliated; a rostrum may have been present but if so it was probably a small one, for shell laminae visible are not noticeably projected backward at the apex.

Shell Structure: Shell substance apparently not completely preserved on any specimen; maximum thickness measures 2 mm on flank of median rib USNM 147231; on specimens over 20 cm in length shell in areas between median and inner ribs was probably between 2 and 3 mm thick; shell thins laterally from median rib. Shell laminated, consisting of two opposing sets of laminae which define inner and outer shell layers that are not easily distinguished macroscopically. Relationships of layers are shown in fig. 4 and on Pl. 4, figs. 1 and 2; laminae of inner layer incline upward and forward in longitudinal sections, upward and outward in transverse sections; in corresponding sections laminae of outer layer incline downward and forward, and downward and outward. Laminae of upper layer pass dorsally into tubercular structure which may occupy all of this layer or as little as the upper third. Degree of tuberculation apparently varies among gladii and in

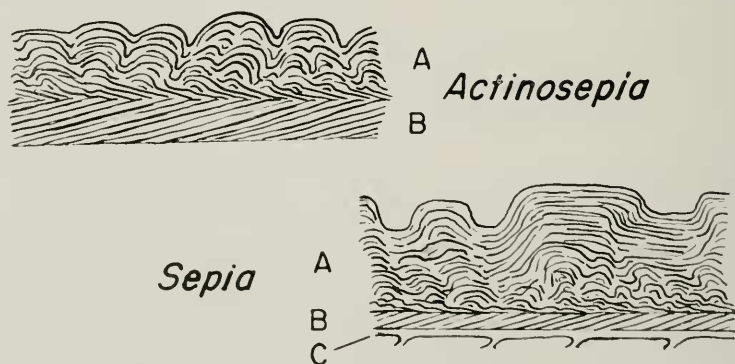


Figure 4. Generalized diagram comparing shell layers of *Actinosepia* with those of dorsal shield of *Sepia* cuttlebone. A. Tuberculate outer layer, the "Rückenplatte" of Appellöf; B. Inner layer, the "Mittelplatte" of Appellöf; C. "Innenplatte" of Appellöf, part of the sepüid pad and not present in *Actinosepia*.

different parts of same gladius. Where outer layer thickest, along median rib, its non-tuberculate part is thickest; as layer thins laterally tuberculation becomes progressively more complete.

Growth lines and ridges are most distinct on surfaces at and adjacent to the juncture of inner and outer layers; growth lines are apparently the edges of laminae along the juncture of the layers, or their impressions on surfaces of laminae of the opposing layer; broader rounded ridges are small flexures which appear restricted chiefly to the basal non-tuberculate part of the upper layer; ridges not well defined on inner layer, usually discernible at or near juncture with outer layer and probably are reflections of flexures in latter. Ridges parallel ends of laminae and no doubt formed at growing edge of shell.

Shell material organic, corneous, slightly to moderately impregnated with calcium carbonate. Treatment with ten per cent HCl shows some differential etching of laminae with slight to moderate efflorescence; shell eventually breaks down to fine bits and plates of organic matter. Inner layer contains more organic matrix and is less calcareous than the outer. Landes (1940, p. 181) states that "the calcareous layers of the shell show distinct growth lines. . . . The horny layers show no trace of the circumferential growth lines. . . ." The inner shell layer which generally lacks growth ridges or lines except at its juncture with the outer layer appears more "horny" than the latter, but to distinguish the outer layer as calcareous is misleading. In none of the specimens does the degree of impregnation with calcium carbonate approach that of the tuberculate dorsal shield of *Sepia*. The gladius of *A. canadensis* was tough but flexible, no part of it was calcified enough to be rigid.

The microstructure of convergent laminae in the shell shows that the inner layer was deposited from below and the outer layer from above and indicates that the gladius was formed in a shell sac, as it is in *Sepia*. The structural similarity between the dorsal shield of a sepiid shell and the gladius of *A. canadensis* becomes evident on comparing the latter with Appellöf's (1893) structural analysis of the shell of *Sepia*. After dividing the cuttlebone into dorsal shield and pad, Appellöf (1893, p. 8-19) describes the structure within the dorsal shield, recognizing three distinctive layers, the dorsal plate (Rückenplatte), middle plate (Mittelplatte) and inner

plate (Innenplatte). The dorsal plate is the thicker and characteristically has tubercular structure; shell laminae at the base of the dorsal plate can be seen to incline downward laterally and forward (fig. 4). The dorsal plate thins toward the edges of the dorsal shield, it grows "by the apposition of new layers on its upper side." (Appellöf, p. 19). The much thinner middle plate grows from the underside, its laminae incline upward and outward. The dorsal and middle plates of *Sepia* are structurally nearly identical to the outer and inner layers, respectively, of the *Actinosepia* gladius, although they differ in their relative thickness and the degree of calcification.

The inner plate of the dorsal shield of *Sepia* is complex in structure; Appellöf (p. 20 and 29) observed that the pad lamellae, or "Septa," pass into it without a break; it is thus distinct from the other two layers of the dorsal shield and essentially a part of the pad. Absence of a pad in *Actinosepia* conceivably could be due to the fact that the delicate pads are relatively easily destroyed, but if a pad was present some remnant of the inner plate should remain on the better-preserved specimens. The fact that the *Actinosepia* gladius was flexible suggests that any buoyancy apparatus the animal may have had attached to it would also have been flexible; attachment of a rigid, delicate structure like the pad of *Sepia* to a flexible plate has obvious functional drawbacks.

Shape and convexity, shell structure and dorsal ornament are the principal similarities between the sepiid cuttlebone and the gladius of *Actinosepia*. A less significant, probably superficial, similarity is the pattern of radiating ribs present in some recent and fossil sepiids. These are broad, flat-topped and generally three in number.

Remarks: Whiteaves' four specimens differ enough from most other specimens of *Actinosepia* to question whether they may be specifically distinct. On these four specimens the angle between the median rib and the inner rib varies from 5.5 to seven degrees; on the gladius from the Bearpaw Shale in Montana, USNM 147231, the same angle is between six and seven degrees. In all other specimens on which it could be measured accurately this angle is more than 7.5 degrees and in the Fox Hills specimens it is consistently in the eight- to nine-degree range. The median-outer rib angle does not exceed 10° in Whiteaves specimens but is

12° to 15° in other specimens. A general trend of increasing rib angles with decreasing geologic age is broken by Landes mold, GSC 19888, from the Bearpaw Shale which has a median-inner rib angle of 8 to 8.5 degrees and a median-outer rib angle of 12°. Too little is known about variation within or between populations of *A. canadensis* to warrant specific separation into two groups on the basis of rib angles alone. There may be slightly finer tuberculate ornament on the Whiteaves specimens but the few scattered remnants of the inner tuberculate laminae preserved are inadequate to demonstrate this conclusively. A better representation of specimens of *Actinosepia* from a number of horizons is needed before a meaningful evaluation can be made of the rather slight differences apparent in the known specimens.

Types: Whiteaves (1897, p. 459) singled out one of the specimens on which he based *A. canadensis* as "The most perfect of the four . . .," illustrating it with a recognizable line-drawing and basing most of the particulars of his description on it. This is interpreted to be an expression equivalent to the stated designation of a "type" under Article 73b of the 1961 International Code of Zoological Nomenclature; the specimen, GSC 5379, is therefore the holotype and the remaining three specimens, GSC 5379a to c, paratypes.

Specimens on which this redescription is based are listed above under the heading *Material and Measurements*. Of these, GSC 19888 is listed as a hypotype by the Geological Survey of Canada; it is the specimen on which Landes based his supplemental description of *A. canadensis*.

RELATIONSHIP TO THE SEPIIDS

The similarities of shape and structure between the gladius of *Actinosepia* and the sepiid cuttlebone can be attributed to parallelism resulting from the adoption of sepiid habits by a branch of the trachyteuthid stock. At our present level of knowledge it is reasonable to consider *Glyphiteuthis* and *Actinosepia* divergent end members of the trachyteuthids, the former tending toward reduction and attenuation of the gladius, the latter toward increasing its breadth, convexity, and strength—that is, becoming more

sepiid-like. It is also reasonable to hold that no true sepiids had yet appeared at this time (Late Cretaceous), for unless unequivocal evidence of a calcified pad in *Voltzia* can be demonstrated it cannot be considered a sepiid.

Rejecting *Voltzia* as a sepiid reinstates the long established scheme, introduced by Voltz (1830) and elaborated on by many, but most significantly by Naef (1921, 1922), of deriving sepiids from a belemnoid stock, according to Naef, through the succession *Belemnosella*–*Spirulirostra*–*Spirulirostrina*–*Belosepia*–*Sepia*. The forms chosen to represent intermediate stages between belemnoids and sepiids are characterized by rostra with impressions or remnants of a short curved phragmocone; these range in age from Eocene to Miocene, but *Belosepia*, Naef's critical end member of chain, did not survive the Eocene. Wagner (1938, p. 197) describes *Sepia agriensis*, a gladius preserving what appear to be remnants of a pad, from the Late Eocene, Ludian, and well-preserved cuttlebones are known from the mid-Oligocene, Rupelian (*S. kiscellensis* Wagner, *S. harmati* Szörényi). Szörényi (1933, p. 188) maintains that Naef's phylogeny is negated by species of *Archaeosepia* from the Eocene, but Wagner (1938, p. 199) believes that neither these nor *Belosepia* gave rise to true sepiids which he states must have been derived at least by earliest Eocene. If, as is probable, *S. agriensis* Wagner is a true sepiid, none of the classically accepted ancestors in Naef's succession are likely to have been the true ancestors.

With the more commonly accepted origins of sepiids open to serious question, the possibility that they were derived from the trachyteuthid stock through an *Actinosepia*-like form deserves consideration. The idea of a trachyteuthid origin for sepiids is not new; it was suggested by Fischer (1887, p. 357) who included trachyteuthids in his Sepiophora and considered them transitional with the Chondrophora (teuthidids). Structurally it is a shorter step from *Actinosepia* to *Sepia* than from any of the small rostrate genera of the Eocene-Miocene to *Sepia*. The expanded, convex, dorsally tuberculate gladius is there; it lacks, chiefly, greater calcification and the pad.

Functionally the two latter features go hand in hand, rigidity of dorsal shield and a calcified pad. *Actinosepia* may well have had a buoyancy apparatus in soft tissues under its flexible gladius;

if so the step from trachyteuthid to sepiid would entail primarily an increase in rigidity of the shell through greater calcification.

Szörényi (1933, p. 185) mentions that in some of the specimens of *Sepia harmati* the pad has survived in the form of a carbonized substance; judging from her description the only calcified remains of the pad are the bases of pad-lamellae adhering to the inner plate (= Innenplatte of Appellöf) on one specimen. This may be an artifact of preservation, but it may also reflect only partial calcification of the pad at this stage in sepiid evolution.

As an alternative working hypothesis the possibility of deriving sepiids from trachyteuthids has the advantage of starting back in the Late Cretaceous with a coleoid that apparently already had adopted the sepiid way of life and in addition possessed a dorsal shield of very nearly identical structure. This is considerably more than can be said for such forms as *Spirulirostra*, *Beloptera* and the like, whose shells feature the gradual diminution of rostrum without concomitant development of the dorsal shield, and without any changes in the phragmocone that approach very closely the laminate and trabeculate pad of *Sepia*. Direct derivation of the pad from the phragmocone is a possibility but it is not a necessity; the pad could just as readily have been formed by resumption of calcium carbonate secretion in tissues much changed in structure but essentially homologous with those that in past periods had secreted a true phragmocone.

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PLATES

PLATE 1.

Actinosepia canadensis Whiteaves

Fig. 1. Holotype (GSC 5379), dorsal aspect; $\times \frac{1}{2}$. The white lines are Whiteaves'; acuminate tips shown for growth lines on lateral ribs are incorrect, the gentle flexures across the ribs are correctly shown by the four white lines in lower right.

Fig. 2. Holotype (GSC 5379), detail of dorsal surface showing remnant (upper left to lower right) of outer tuberculate shell layer; $\times 8$.

Fig. 3. Holotype (GSC 5379) transverse profile at A, $\times \frac{1}{2}$.

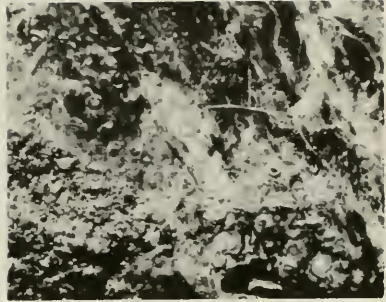
Fig. 4. Characteristic *Actinosepia* concretion from the Fox Hills Formation (YPM 24809) $\times \frac{1}{2}$.

Fig. 5. YPM 24809; transverse profile at A, $\times \frac{1}{2}$.



1

A



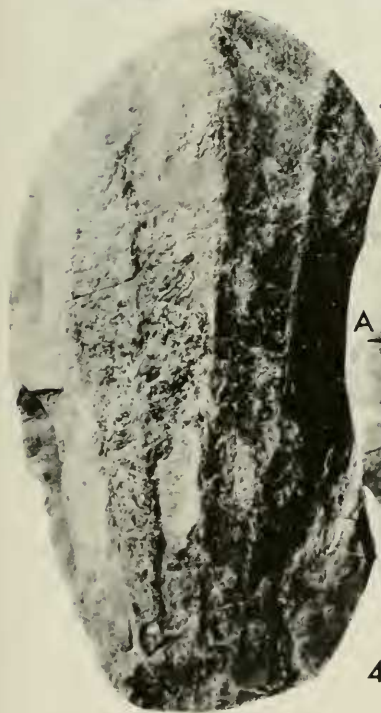
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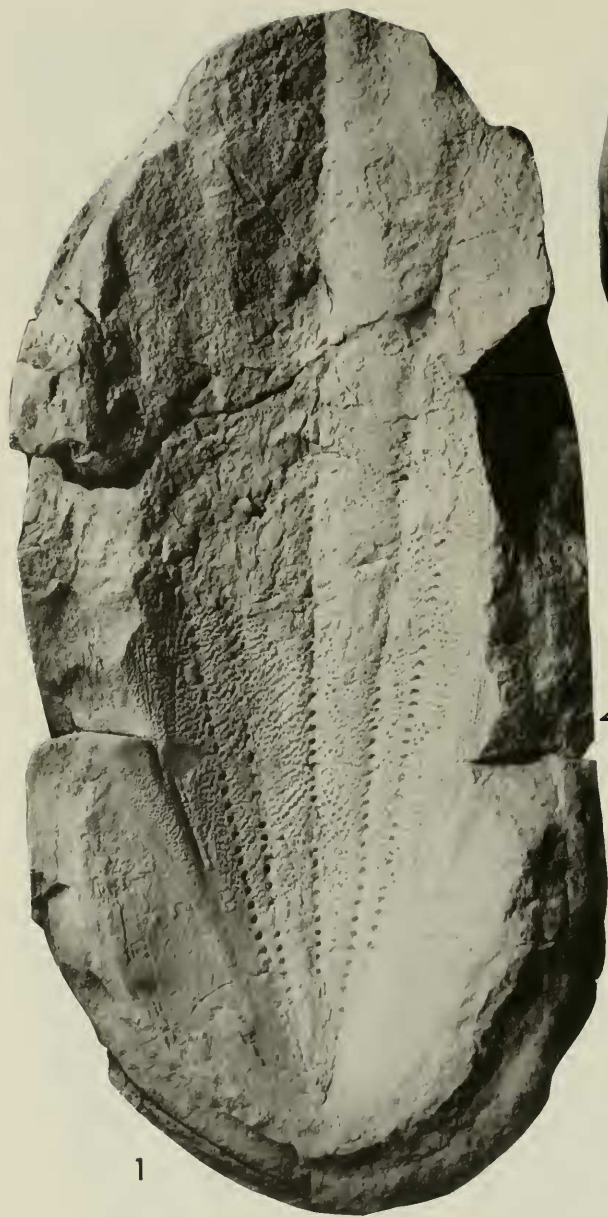


5



A

4



A

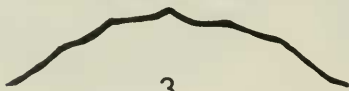


PLATE 2.

Actinosepia canadensis Whiteaves

Fig. 1. External mold from Bearpaw Shale near Manyberries, Alberta, (GSC 19888); $\times \frac{1}{2}$.

Fig. 2. Cast of GSC 19888, profile view of left side; $\times \frac{1}{2}$.

Fig. 3. Cast of GSC 19888, transverse profile at A; $\times \frac{1}{2}$.